Great Basin Naturalist 55(3), © 1995, pp. 304–314

ADDITIONS TO KNOWLEDGE OF PALEOCENE MAMMALS FROM THE NORTH HORN FORMATION, CENTRAL UTAH

Richard L. Cifelli[1], Nicholas J. Czaplewski[1], and Kenneth D. Rose[2]

ABSTRACT.—The distinctive but inadequately known Paleocene faunas of central Utah are significant in that they sample a time interval not well represented by sequences in other areas. New materials from the Wagon Road (late Puercan) and Dragon (early Torrejonian) local faunas, North Horn Formation, provide additional information on the composition of the assemblages and systematics of included mammal taxa. The proteutherian *?Propalaeosinopa* is recorded, for the first time, from the Wagon Road fauna, indicating a significant extension for the enigmatic family Pantolestidae, otherwise first known from the Torrejonian. Associated premolars of *Aphronorus simpsoni*, a pentacodontid proteutherian from the Dragon fauna, indicate that the species is more distinct from its Torrejonian congener, *A. fraudator*, than previously suspected. New materials of *Desmatoclaenus hermaeus* uphold the synonymy of this species with *D. paracreodus* and permit more adequate definition of the genus with respect to the arctocyonid *Loxolophus* and the phenacodontid *Tetraclaenodon*; because *Desmatoclaenus* appears to share derived morphology with *Loxolophus*, we refer it to the basal condylarth family Arctocyonidae. The periptychid condylarth *Haploconus*, represented in the Wagon Road fauna by the geologically oldest described species of the genus, *H. elachistus*, is shown to be distinctive in the configuration of lower molars and premolars; *H. elachistus* appears to be more primitive than species known from the Torrejonian of New Mexico. Some features of *Haploconus* are suggestive of the Conacodontinae, a distinctive clade of diminutive periptychids.

Key words: Paleocene, North Horn Formation, Puercan, Torrejonian, Dragon local fauna, Wagon Road local fauna, Mammalia.

Paleocene mammals were first reported from the North Horn Formation, Emery and Sanpete counties, UT, by Gazin (1938). Further fieldwork resulted in the recovery of additional taxa, interpreted as representing two faunas, from two main localities (Gazin 1939, 1941). In subsequent years, additional sites in the region have yielded further specimens, including more taxa and a third faunal assemblage (Spieker 1960, Van Valen 1978, Tomida and Butler 1980, Tomida 1982, Robison 1986, Archibald, Rigby, and Robison 1983). Three assemblages are currently recognized, the Gas Tank, Wagon Road, and Dragon local faunas (Robison 1986). On the basis of the latter two, a "Dragonian" land-mammal age was initially established (Wood et al. 1941). Later work, including magnetic stratigraphy and biostratigraphic comparisons, suggests that the Gas Tank and Wagon Road faunas are Puercan and the Dragon fauna Torrejonian in age (Tomida and Butler 1980, Tomida 1981, Robison 1986). Archibald et al. (1987) tentatively assigned the Gas Tank to Pu2 (*Ectoconus / Taeniolabis taoensis* interval zone), Wagon Road to Pu3 (*Taeniolabis taoensis / Periptychus* interval-zone), and Dragon to To1 (*Periptychus / Tetraclaenodon* interval-zone). Both Pu2 and Pu3 are interpreted to occur within magnetic polarity chron 29N (Butler and Lindsay 1985); the Dragon fauna is considered to lie within anomaly 27N (Tomida and Butler 1980).

The Paleocene mammals of central Utah are of special interest in both temporal and geographic contexts: they fall within a time interval not well represented elsewhere, and they lie geographically between the classic sequence of the San Juan Basin, NM, and faunas from more northerly parts of the Western Interior (cf. Archibald et al. 1987: fig. 3.1). Mammals from the Paleocene of the North Horn Formation are not, in general, well known. We describe herein newly collected materials that provide further details on the morphology and systematics of some of the included taxa.

The approximate locations of the major mammal sites in the Paleocene part of the North Horn Formation, taken from data presented by Gazin (1941) and Robison (1986), are given in Figure 1. The materials described

---

[1] Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, OK 73019.
[2] Department of Cell Biology and Anatomy, Johns Hopkins University School of Medicine, 725 North Wolfe St., Baltimore, MD 21205.

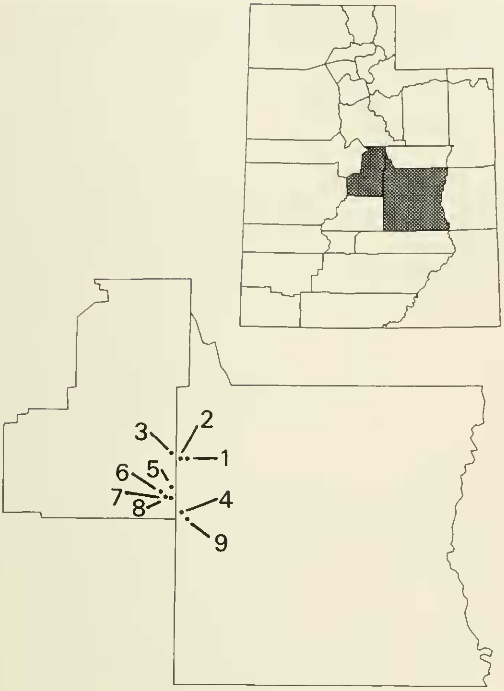

Fig. 1. Approximate locations of mammal-bearing sites in Paleocene part of North Horn Formation, Emery and Sanpete counties, UT; data from Gazin (1941) and Robison (1986). Localities, Dragon local fauna: Dragon Canyon (1). Wagon Road local fauna: Wagon Road (2), Wagon Road Ridge (3). Gas Tank local fauna: Gas Tank Hill (4), Dairy Creek (5), Jason Spring (6), Ferron Mountain (7; probably equivalent to OMNH V829), Blue Lake (8), and Sage Flat (9).

herein were collected in 1993–94, through surface prospecting methods. With one exception, all specimens are from the classic Dragon Canyon (Dragon local fauna; ?To1) and Wagon Road (Wagon Road local fauna; ?Pu3) sites described by Gazin (1941). The exception is a specimen assigned to *Ectoconus ditrigonus* (OMNH 28111), collected by Jon Judd of Castle Dale, UT, at a site south of Ferron Mountain. The site, OMNH V829, is probably the same as Robison's (1986) Ferron Mountain locality (Gas Tank local fauna; ?Pu2).

The following abbreviations are used for institutions cited in the text: BYU, Brigham Young University, Provo, UT; OMNH, Oklahoma Museum of Natural History, Norman; USNM, National Museum of Natural History, Washington, DC. Measurements, in mm, are as follows: L, anteroposterior length; W, transverse width; WTal, transverse width of talonid; WTri, transverse width of trigonid.

DESCRIPTIVE ACCOUNTS

Order Proteutheria

Family Pantolestidae Cope, 1884
?*Propalaeosinopa* sp.

Figs. 2A–B

MATERIAL.—OMNH 27681, fragment of right dentary bearing the talonid of P_4 (WTal = 1.5) and complete M_1 (L = 2.8, WTri = 1.8, WTal = 1.8).

LOCALITY AND HORIZON.—OMNH V800, "Wagon Road" locality (Gazin 1941, Robison 1986); Wagon Road local fauna, late Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—The dentary fragment includes the anterior root of P_4 and the anterior root of M_2. The anterior root of P_4 is bowed forward as in pentacodontids and most pantolestids, and its placement indicates that P_4 was relatively long, longer than M_1. The posterior mental foramen is large and is positioned between the posterior root of P_4 and the anterior root of M_1. The talonid of P_4 includes a large hypoconid and a small entoconid; these two cusps are united by a small, thin postcristid, forming a small talonid basin. The apex of the hypoconid is on the midline of the tooth, at the posterior termination of a cristid obliqua that angles lingually toward the front; the postcristid is oriented almost perpendicular to the cristid obliqua. Posterior to the postcristid and separated from it by a tiny transverse basin, a small cuspule (hypoconulid?) is present; this cuspule is connected to the hypoconid by a thin ridge. A tiny entoconulid, not connected to the other cusps, is present at the lingual base of the talonid basin.

The trigonid and talonid of M_1 are of equal width; the trigonid is distinctly higher than the talonid, though the tooth is moderately worn. The protoconid and metaconid are both triangular in occlusal outline and of equal occlusal area; the protoconid is the taller of the two cusps. The paraconid is small, low, and transversely oriented. Anterior and posterior carnassial notches are present in the paracristid and protocristid, respectively. Because of the transverse orientation of the paraconid, the paracristid forms an obtuse angle, with its apex at the anterior carnassial notch. A short anterior cingulum, which disappears at the anterolingual corner of the tooth, is present.

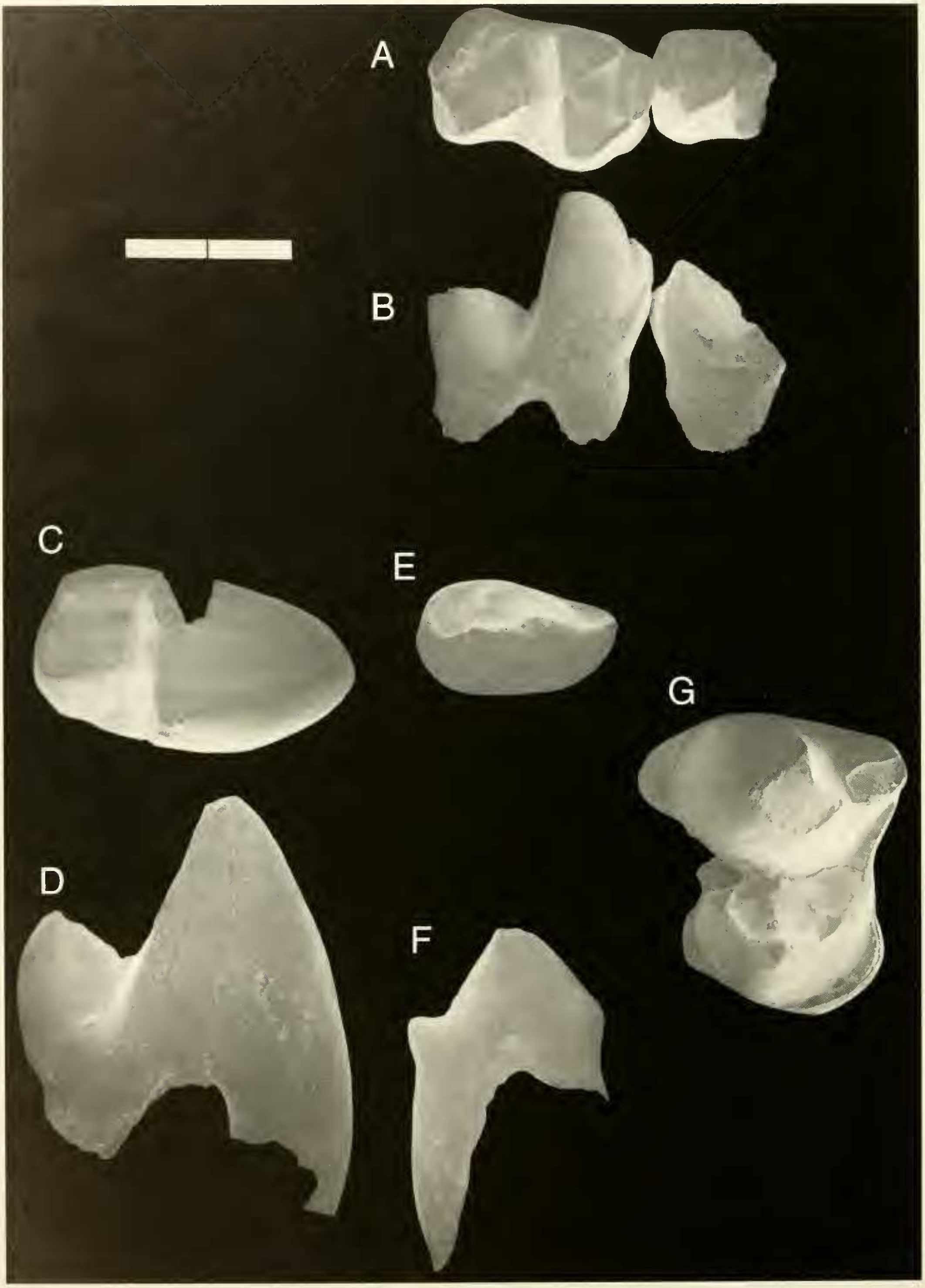

Fig. 2. Proteutheria from the North Horn Formation. A, B, P_4–M_1 of *Propalaeosinopa* sp. (OMNH 27681) in occlusal (A) and labial (B) views. C–G, *Aphronorus simpsoni* (OMNH 27667): C, D, right P_4 in occlusal and labial views, respectively; E, F, right P_3 in occlusal and labial views, respectively; G, left P^4 in occlusal view. Scale bar represents 2 mm; tooth roots and jaw fragments have been eliminated to improve clarity.

The posterior wall of the trigonid is planar; the cristid obliqua meets the base of the posterior wall of the trigonid below the posterior carnassial notch. Although it has been mostly obliterated by wear, an entoconulid (or at least an entocristid) appears to have been present anterior to the entoconid.

Of described species, OMNH 27681 most resembles the Torrejonian *Propalaeosinopa diluculi* (which we tentatively regard as distinct from *P. albertensis* following Rose 1981; see discussion in Van Valen 1967). However, the Utah taxon differs in several respects. The posterior mental foramen is more anteriorly located than in figured specimens of *P. diluculi* (Simpson 1936: fig. 3; Krause and Gingerich 1983: figs. 8, 9). M_1 of OMNH 27681 is long and narrow relative to the corresponding tooth of *P. diluculi*: it slightly exceeds published size ranges (Simpson 1937a, 1937b, Krause and Gingerich 1983) in length but not width. In the Utah taxon the cusps of M_1 are somewhat more robust and the postvallid wall more obliquely oriented with respect to the long axis of the tooth; the paracristid is higher, and the metaconid lower, than in *P. diluculi*. The talonid of P_4 is broader and more basined than in *P. diluculi* (or other species of the genus). We regard the specimen from the North Horn Formation as representing a distinct species, but materials in hand are inadequate to properly diagnose and circumscribe it. Gazin (1941) briefly described two morphs, represented by upper molars, as generically undetermined pantolestids; both were from the Dragon local fauna. Of these, he found pantolestid "a" to compare favorably with *Bessoecetor* (=*Propalaeosinopa*), differing from "*B. thomsoni*" (=*P. diluculi*) in being slightly larger and in a few morphological details. It is possible that pantolestid "a" and OMNH 27681 represent the same species, although we point out that they derive from different horizons in the North Horn Formation. Differential representation precludes direct comparison with OMNH 27681.

If referral of the newly recovered specimen to *Propalaeosinopa* is correct, it represents the oldest record of the genus and of the family Pantolestidae, a somewhat aberrant group of enigmatic affinities. The new occurrence is estimated to be late Puercan (Pu3) in age; the genus and family are otherwise first known from the late Torrejonian (To3; Archibald et al. 1987). In this context, we note that several morphological details show the North Horn taxon to be distinct, at the species level at least, from described species; when better known, it may prove to be generically separable.

Family Pentacodontidae
(Simpson, 1937) Van Valen, 1967
Aphronorus simpsoni Gazin, 1938
Figs. 2C–G

NEWLY REFERRED MATERIAL.—OMNH 27667, right dentary fragment with P_{3-4} ($P_3L = 2.4$, $W = 1.4$; $P_4L = 4.0$, $W = 2.5$) and associated left P^4 ($L = 3.3$, $W = 4.1$).

LOCALITY AND HORIZON.—OMNH V799, "Dragon" locality (locality 2 of Gazin 1941: p. 7, fig. 1), Dragon local fauna, early Torrejonian (early or middle Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—OMNH 27667 differs from the type of *A. simpsoni* (USNM 15539) in minor ways but is clearly referable to the species. P_4 is slightly larger than in the type and differs in having a weaker anterior cingulum, which is barely indicated on the anterolingual part of the tooth and is completely absent labial to the keel extending down the anterior face of the protoconid. The minute ridge that extends down the posterior wall of the metaconid (to meet with the cristid obliqua) is lacking; however, the development of this ridge in the type may be due partly to the advanced wear in that specimen. P_4 of OMNH 27667 bears a small but distinct entoconid; this region of the tooth is broken in USNM 15539. The anterior end of P_4 in OMNH 27667 is slightly more developed downward than in USNM 15539, vaguely recalling the more advanced condition seen in *Pentacodon* (Simpson 1937a: 124). Unlike either species of *Pentacodon*, however, the P_4 lacks a basal paraconid, the protoconid is not as inclined posteriorly from base to apex, and the talonid is better developed.

P_3 has not been previously figured or described for *Aphronorus simpsoni*, though this tooth is known for *A. fraudator* (illustrated in outline by Simpson 1937a, Gazin 1941). P_3 of OMNH 27667 is more anteroposteriorly elongate than in *A. fraudator*. The tooth is distinctly two-rooted and is much smaller than P_4; maximum width occurs just posterior to the protoconid. A small talonid basin is developed, with a minute hypoconid and a "cristid obliqua" connected to a ridge running down the posterior flank of the protoconid. A small, short ridge and swelling on the posterolingual flank of the protoconid are suggestive of a metaconid. A faint cingulum is present anterolingually.

No associated upper teeth have been previously described for *Aphronorus simpsoni*, although a few isolated specimens may belong to the species (Gazin 1941, Robison 1986). P^4 of OMNH 27667 is broken near the paraconule and at the lingual edge of the tooth, between the cingulum at the base of the protocone and the lingual root; the labial side of the metaconid is also damaged. Three roots are present. The tooth, although similar to P^4 of *A. fraudator*, differs in several respects. The parastyle is absent; a small paraconule is present; a metaconule as such is lacking, although there is a vague swelling of enamel in this position. The basal protoconal cingula show no tendency to develop cuspules, as they do in *A. fraudator*, and the metacone is much smaller in size, relative to the paracone, than in that species. The labial cingulum of P^4 in OMNH 27667 is also less developed than in *A. fraudator*.

Aphronorus simpsoni was diagnosed as distinct from the comparatively well-known *A. fraudator* mainly on the basis of differences in proportions of P_4 and the lower molars (Gazin 1941). OMNH 27667, which includes teeth previously unreported for *A. simpsoni*, shows that it is further distinct in having a somewhat more elongate P_3; P_4 has a narrower, smaller-basined talonid. P^4 differs from that of *A. fraudator* in several respects, including the lack of a metaconule and parastyle, and the much lesser development of the metacone. Considering the specializations of the posterior premolars in pentacodontids (Simpson 1937a) and the possibility that they represent a relatively archaic group (Van Valen 1967), it is difficult to judge which conditions are apomorphous, although some of the states possessed by *A. simpsoni* (e.g., smaller P_4 talonid; P^4 with small metacone and no metaconule) would appear—by comparison to more primitive Eutheria—to be primitive. The Tiffanian species *A. orieli*, known by remarkably complete specimens (Gingerich et al. 1983), appears to be considerably more advanced, with greatly expanded crushing surfaces (particularly the protocone) on P^4.

Order Condylarthra
Family ?Arctocyonidae
(Giebel, 1855) Murray, 1866
Desmatoclaenus hermaeus Gazin, 1941

Fig. 3A

NEWLY REFERRED MATERIAL.—OMNH 27682, associated skull and jaw fragments with broken right and left P^4 (right $P^4L = 6.5$), right M^{1-3} ($M^1L = 7.3$, $W = 8.6$; $M^2L = 7.3$, $W = 11.0$; $M^3L = 6.2$, $W = 8.7$), left M^{2-3} (M^2 broken, $L = 7.4$; $M^3L = 6.0$, $W = 8.8$), left M_1 ($L = 8.8$, $WTri = 7.2$, $WTal = 7.4$), talonid of right M_2 ($W = 6.4$), trigonid of left M_2 ($W = 6.0$), and talonid of right M_3 ($W = 5.2$).

LOCALITY AND HORIZON.—OMNH V800, "Wagon Road" locality (Gazin 1941, Robison 1986); Wagon Road local fauna, late Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—P^4 has distinct conules, with the paraconule being taller than the metaconule. These cusps have not previously been noted for P^4 of the species, perhaps because of wear on the type specimen (USNM 16202; see Gazin 1941: fig. 19; West 1976: fig. 2). The upper molars have a labial cingulum that is continuous. Interruption of the ectocingulum at the base of the paracone was cited as a generic character of *Desmatoclaenus*. However, the cingulum is complete in other specimens, such as BYU 3800 (Robison 1986: pl. 2, fig. 10), and we regard this as a feature that is intraspecifically variable. M^3 bears a small but distinct cingular hypocone, another character that is apparently variable in the species (Gazin 1941: figs. 19, 20; Robison 1986). The only variation worthy of note in the lower dentition of OMNH 27682 is the hypoconulid of M_3, which apparently projected posteriorly as a distinct lobe, unlike the condition seen in USNM 16202 (Gazin 1941: fig. 19).

Gazin (1941) originally described two species of *Desmatoclaenus*, *D. hermaeus* and *D. paracreodus*, both from the Wagon Road fauna. West (1976) synonymized the two, a view apparently shared by Tomida and Butler (1980), but Robison (1986) recognized them as distinct and reported additional materials of both species from other localities. In the original diagnosis (Gazin 1941), *D. paracreodus* was said to be larger than *D. hermaeus*, with the lingual portion of upper molars more inflated and with a relatively larger M^3, bearing a better-

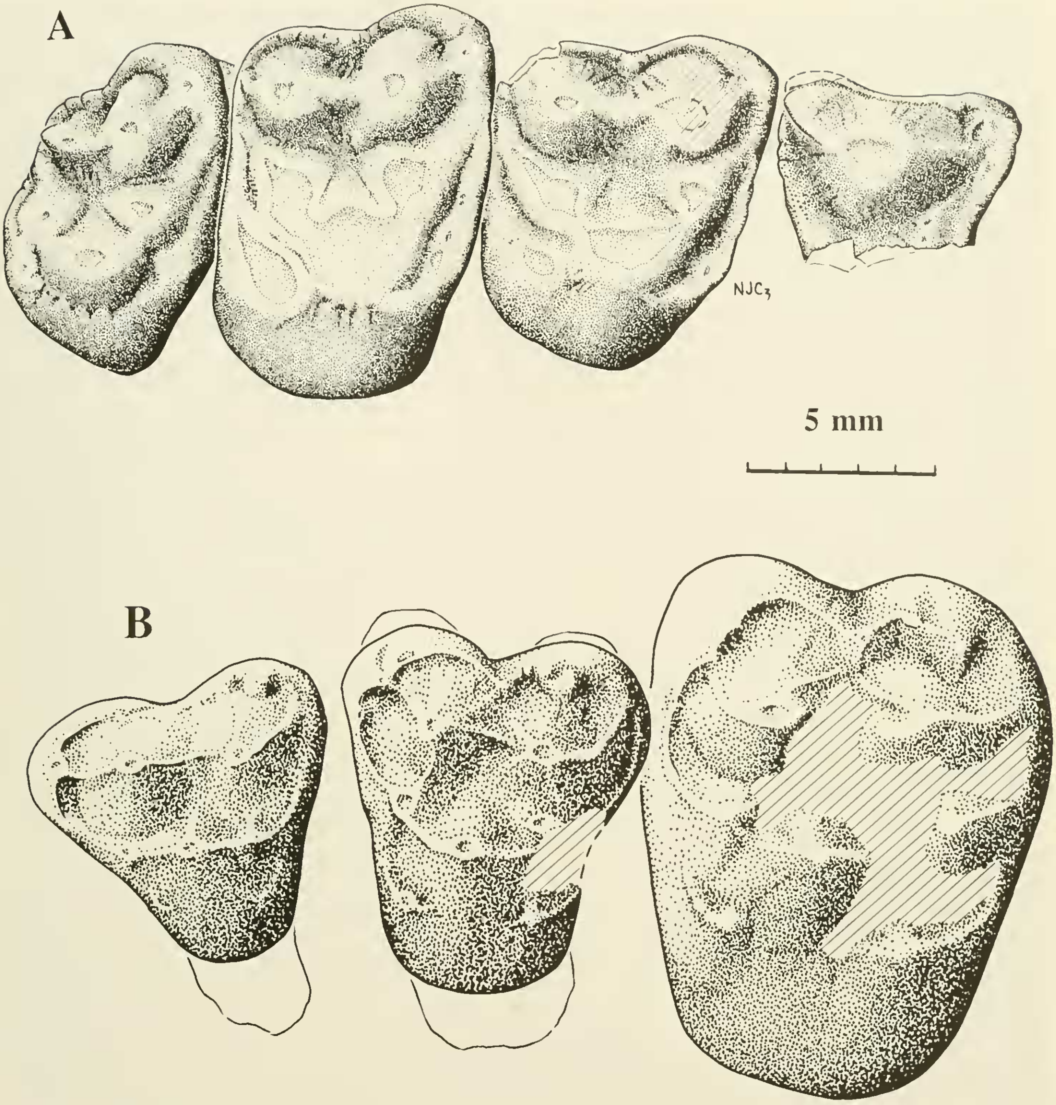

Fig. 3. ?Arctocyonidae and Periptychinae from the North Horn Formation. A, right P^4–M^3 of *Desmatoclaenus hermaeus* (OMNH 27682) from the North Horn Formation; base of M^2 restored from contralateral tooth of same specimen, and maxilla eliminated to improve clarity; B, left $dP^{3–4}$ and M^1 of *Ectoconus ditrigonus* (OMNH 28111) in occlusal view; maxilla eliminated to improve clarity.

developed hypocone. As shown by West (1976), these differences in size and morphology are both minor and inconsistent. In this context, we note that $M^{1–2}$ of OMNH 27682 are relatively small (a supposed character of *D. hermaeus*), yet M^3 is proportionately large, with a well-developed hypocone (characters cited for *D. paracreodus*). We follow West (1976) in regarding the species as synonymous.

In the original diagnosis and discussion of *Desmatoclaenus*, Gazin (1941) compared the genus with *Tetraclaenodon* and *Protogonodon*, as the latter taxon was then conceived (Matthew 1937, Simpson 1937a). Van Valen (1978) placed "?*P.*" *protogonioides* (cf. Matthew 1937)—originally referred (Cope 1882a), in part, to the genus *Mioclaenus*—in *Desmatoclaenus*, adding to the genus two additional species, *D. dianae* and *D. mearae*; *Protogonodon* was synonymized with *Loxolophus*. We are in agreement with these assignments; *D. protogonioides* is relatively well represented and adds significantly to knowledge of the genus. Thus recognized, *Desmatoclaenus* is distinct from *Loxolophus* in having stronger protocones on P^{3-4}; better-developed, more lingually placed hypocone on M^{1-2}, with hypocone occasionally distinct on M^3; and paraconid of lower molars placed more posterolingually and closely appressed to the metaconid. *Desmatoclaenus* differs from *Tetraclaenodon* in having less molarized premolars (a metacone is lacking on P^{3-4}; the trigonid is poorly developed and a talonid basin is lacking on P_4), upper molars lacking mesostyle and with lesser development of the hypocone; and lower molars with more distinct, anteriorly placed paraconid.

Gazin (1941) considered *Desmatoclaenus* to be structurally intermediate between the archaic ungulate "*Protogonodon*" (then considered a creodont) and *Tetraclaenodon*, a primitive phenacodontid; the differential comparisons presented above uphold this view. Subsequent workers have referred *Desmatoclaenus* to the Arctocyonidae on the one hand (Van Valen 1978, Cifelli 1983) or the Phenacodontidae on the other (Simpson 1945, West 1976, Robison 1986). The positioning of the upper molar hypocone somewhat more lingually in *Desmatoclaenus* than in *Loxolophus* is vaguely reminiscent of the presumably derived condition in the Phenacodontidae; similarly, the low, bunodont cusps bearing mainly flat, apical wear are similar to conditions generally obtained in members of that family. *Desmatoclaenus* may well be a transitional taxon, but in the absence of compelling evidence in the form of synapomorphies, we here tentatively retain it in the Arctocyonidae. In this context, we note that the referred species *D. protogonioides* apparently has a reduced anterior dentition, a condition shared with loxolophine arctocyonids (Cifelli 1983).

Family Periptychidae Cope, 1882

Anisonchus ?oligistus Gazin, 1941

Fig. 4A

NEWLY REFERRED MATERIAL.—OMNH 27679, right M^3.

LOCALITY AND HORIZON.—OMNH V800, "Wagon Road" locality (Gazin 1941, Robison 1986); Wagon Road local fauna, late Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION.—OMNH 27679 is missing the lingual base of the crown and enamel from the posterior margin of the tooth; its estimated L is 3.1. This specimen is appropriate in size for only two of the four species of *Anisonchus* reported from the North Horn Formation (Gazin 1941, Robison 1986); OMNH 27679 differs from M^3 referred to *A. athelae* (including *A. eowynae*; Robison 1986) and is tentatively referred to *A. oligistus*, for which M^3 was not previously known. Although the tooth is incomplete and worn, it can be seen that the anterocingulum was relatively weak and lacked a pericone. Similarly, the hypocone was weak in comparison to the condition in *A. athelae*, being more similar to the larger *A. dracus* in this respect. The pattern of wear suggests that both paraconule and metaconule were present, placed near the base of paracone and metacone, respectively.

Haploconus elachistus Gazin, 1941

Figs. 4B–F

NEWLY REFERRED MATERIAL.—OMNH 27670, fragments of mandible with left M_{1-2} ($M_1L = 3.8$, $WTri = 2.7$, $WTal = 2.8$; $M_2L = 3.9$, $WTri = 3.2$, $WTal = 2.9$) and right M_2 ($L = 4.0$, $WTri = 3.1$, $WTal = 3.0$); 27713, fragments of left mandible with P_3 ($L = 4.5$, $W = 2.8$) and a heavily encrusted molar; OMNH 27680, right P_4 ($L = 4.5$, $W = 3.3$).

LOCALITY AND HORIZON.—OMNH V800, "Wagon Road" locality (Gazin 1941, Robison 1986); Wagon Road local fauna, late Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—Available lower premolars (OMNH 27680, 27713) are too worn to determine whether a paraconid was present; Gazin (1941) reported the presence of this cusp on P_3 but not P_4 of *Haploconus elachistus*. The protoconid is a large, inflated cusp, particularly on P_4. A talonid crescent extends posteriorly from the lingual base of the protoconid, curving labially at the posterior margin of both P_3 and P_4. The metaconid of lower molars is nearly as tall as the protoconid and is transversely aligned with that cusp; a weak paracristid descends anterolingually from the protoconid, terminating in a small paraconid, which lies in a median position. As described by Gazin (1941), the pre-entocristid is taller than the cristid obliqua. The entoconid forms a distinct pillar and projects somewhat on the

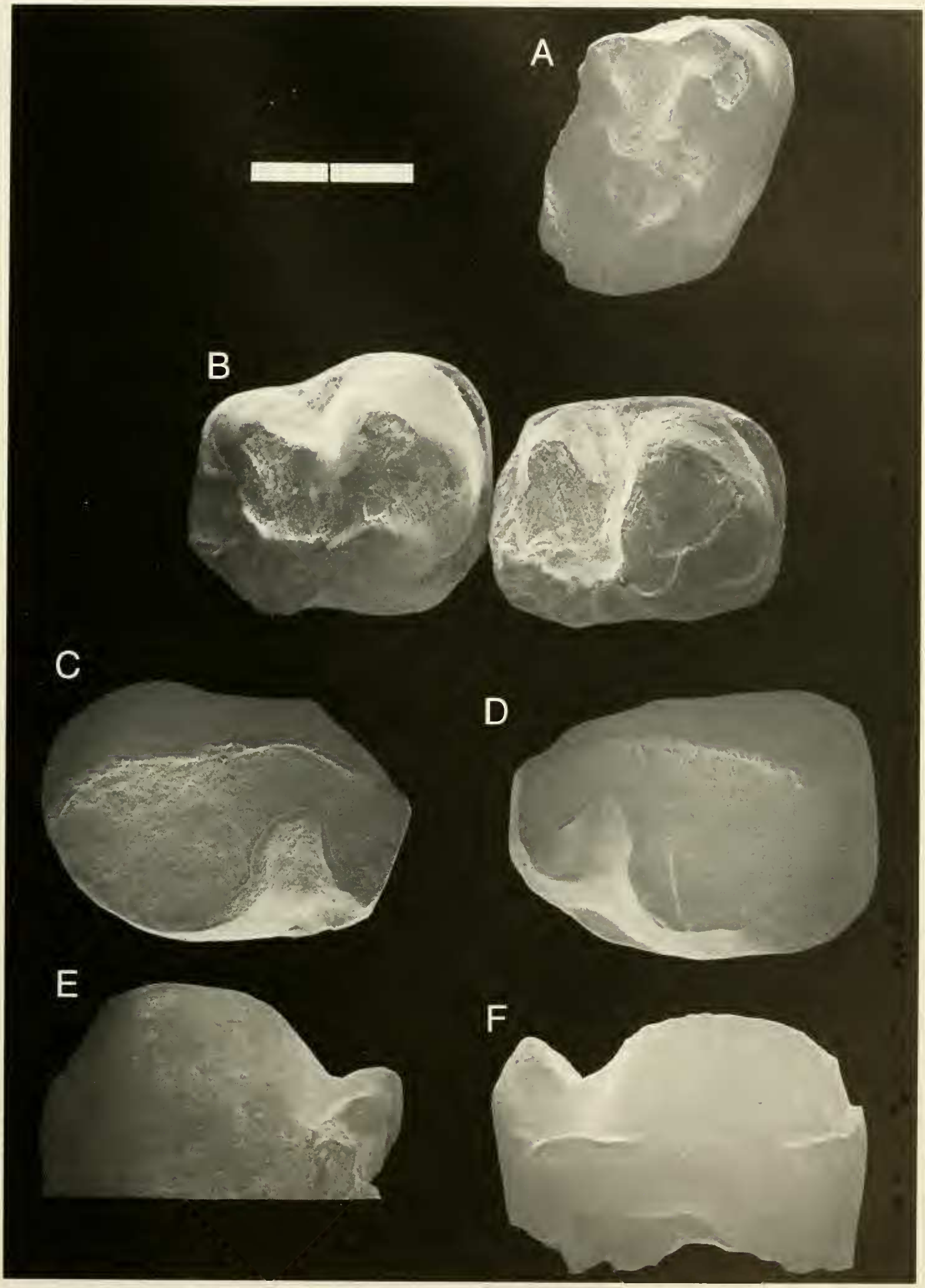

Fig. 4. Anisonchinae from the North Horn Formation. A, *Anisonchus ?oligistus* (OMNH 27679, right M^3 in occlusal view). B–F, *Haploconus elachistus*: B, left M_{1-2} (OMNH 27670) in occlusal view; C, E, left P_3 (OMNH 27713) in occlusal and labial views, respectively; D, F, right P_4 (OMNH 27680) in occlusal and labial views, respectively. Scale bar represents 2 mm; tooth roots and jaw fragments have been eliminated to improve clarity.

lingual side of the tooth; the hypoconulid forms a fingerlike projection at the back of the tooth and is somewhat lingual in position, an appearance emphasized in later wear stages.

Two species of *Haploconus*, *H. angustus* and the larger *H. corniculatus*, are recognized from the Torrejonian (To2; Archibald et al. 1987) of the San Juan Basin, NM (Matthew 1937). The apparent last record of *Haploconus* is represented by a single molar, of uncertain specific affinities, from Swain Quarry (To3?; Archibald et al. 1987), WY (Rigby 1980). The genus is otherwise known only from the North Horn Formation. Gazin (1939) described *H. inopinatus* from the Dragon fauna, later adding a second species, ?*H. elachistus*, from the Wagon Road (Gazin 1941). More recently, Robison (1986) has reported specimens of *Haploconus* sp. from the Gas Tank local fauna; these materials are of interest in documenting the first appearance of the genus, but unfortunately they are not specifically diagnostic. *H. inopinatus*, of To1 age, is similar in size to the later *H. angustus* but differs from that species in proportions of the upper molars (Gazin 1939). *H. elachistus*, the geologically oldest described species, is smaller than the Torrejonian species and, as noted by Gazin (1941), differs from them in a number of respects. In the lower dentition, P_{3-4} are less inflated than in *H. angustus*. Similarly, the trigonids of lower molars in *H. elachistus* lack the inflated appearance seen in Torrejonian species; a small paraconid is still present, whereas in remaining species the paracristid forms a bladelike surface extending anteriorly from the protoconid and bears no cusp. Lower molars of *H. elachistus* also lack the crenulated or striated enamel and prominent labial cingulum seen in other species. As might be expected, the geologically older *H. elachistus* appears to be more primitive than the Torrejonian species for the characters cited. In this context the apparent presence of a more derived species in the Gas Tank local fauna (Robison 1986) is somewhat surprising.

Haploconus is distinctive in the extreme modification of lower molar trigonids (with reduction to loss of the paraconid) and in the unusual configuration of the talonid in posterior lower premolars (with a lingual rather than labial crescent), characters that are both expressed in *H. elachistus*. The affinities of the genus are puzzling; Gazin (1941), noting the primitiveness of some features of *H. elachistus*, considered the species to be transitional between *Conacodon* and more derived species of *Haploconus*. In retaining unreduced lower molar trigonids and relatively unspecialized lower premolars, species of *Conacodon* are primitive with respect to *Haploconus*. In terms of characters that are probably derived within the context of Condylarthra, *Conacodon*, *Haploconus*, and *Oxyacodon* have a lingually placed hypoconulid and hypertrophied postmetacristid on lower molars, lingually placed hypocone on upper molars, loss of protocone on P^3, and, possibly, a columnar, lingually placed entoconid on lower molars (not clearly seen in all species of *Oxyacodon*). However, the exclusiveness of these characters and their potential status as synapomorphies remain to be established. Archibald, Schoch, and Rigby (1983) have shown that *Conacodon* and *Oxyacodon* represent a distinctive subfamily, Conacodontinae, whose relationship to other periptychids is unclear; further investigation of the position of *Haploconus* with respect to this clade is clearly warranted.

Ectoconus ditrigonus (Cope, 1882)

Fig. 3B

NEWLY REFERRED MATERIAL.—OMNH 28111, fragment of left maxilla with dP^{3-4} and M^1 ($dP^3L = 7.5$, $W = 7.0$; $dP^4L = 7.5$, $W = 8.4$; $M^1L = 9.6$, $W = 13.5$).

LOCALITY AND HORIZON.—OMNH V829, probably the same as Robison's (1986) Ferron Mountain locality; Gas Tank local fauna, middle Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—The deciduous teeth, dP^{3-4}, are markedly smaller than M^1; both have conspicuous parastylar and metastylar lobes. The third deciduous premolar has a roughly triangular occlusal profile and is longer than it is wide. The paracone and metacone are subequal in height; a large parastyle is present almost directly anterior to the paracone. A prominent ridge extends lingually from the parastyle to the protocone, which is nearly as tall as the paracone and metacone; another ridge descends the labial slope of the parastyle, continuing posteriorly as a weak ectocingulum. Labial to the metacone, the stylar shelf broadens; a small cusp, serially analogous (if not homologous) to a similar cusp on upper molars of *Ectoconus ditrigonus* (Osborn and Earle 1895), is present labial to the metacone. A salient postmetacrista descends posterolabially from the apex of the metacone, extending to the posterolabial corner of the tooth. Weak paraconule and metaconule are present on the pre- and postprotocrista, respectively. Faint pre- and postcingulae are present on the lingual slopes of the protocone. The fourth deciduous premolar is more molariform than dP^3, differing from M^1 in having smaller conules and associated cristae, and in the lesser development of the protocone region. The parastyle of dP^4 is more labially placed than on dP^3, and the ectocingulum and cingular cusp better developed than on that tooth; a small mesostyle is also present. The lingual cingulae are strong; pericone and hypocone are present. M^1 is typical of *Ectoconus* and complete description is unnecessary. The ectocingulum is strong and bears both a mesostyle and posterior stylar cusp. The latter is subconical and is connected to the base of the metacone by a low ridge. Paracone, metacone, and protocone are subequal in height; conules are strongly developed and are only slightly lower than the principal cusps.

Ectoconus ditrigonus, the type species, was first described on the basis of material from the San Juan Basin, NM (Cope 1882b). Matthew (1937) reported a second species from the San Juan Basin, *E. majusculus*, considered by Van Valen (1978) to be synonymous with *E. ditrigonus*. The genus is known from several localities, including both Pu2 and Pu3 horizons, in that area (Archibald et al. 1987). Gazin (1941) described the species *E. symbolus* from the Wagon Road (?Pu3) fauna, North Horn Formation. Robison (1986) described additional materials of *E. symbolus* from localities of the Gas Tank fauna, thereby extending the range of the species to ?Pu2, and reported *E. ditrigonus* from two Gas Tank localities. OMNH 28111 can be referred to the latter species on the basis of size (larger than *E. symbolus*) and the presence of a relatively small posterior cusp, connected to the base of the metacone by a low ridge, on the ectocingulum of M^1 (Robison 1986).

Deciduous teeth of archaic ungulates have not been widely described or illustrated, a notable exception being the deciduous premolars of Phenacodontidae (West 1971). To our knowledge, deciduous teeth of Periptychidae have not been previously described, so that there is no basis for comparison with dP^{3-4} of *Ectoconus ditrigonus*.

ACKNOWLEDGMENTS

We are especially grateful to Dale Harber for the cooperation of the U. S. Forest Service. We thank Jon Judd, Monte Swasey, and Scott Madsen for help in the field; Dr. Scott Russell, Noble Electron Microscopy Laboratory, for access to equipment and facilities; and Estelle Miller for preparing the SEM photographs. Drs. David W. Krause, J. David Archibald, and Jeffrey G. Eaton provided invaluable comments that improved the manuscript. Fieldwork was supported by grant number 5021-93 from the National Geographic Society.

LITERATURE CITED

ARCHIBALD, J. D., P. D. GINGERICH, E. H. LINDSAY, W. A. CLEMENS, JR., D. W. KRAUSE, AND K. D. ROSE. 1987. First North American land mammal ages of the Cenozoic Era. Pages 24–76 *in* M. O. Woodburne, editor, Cenozoic mammals of North America: geochronology and biostratigraphy. University of California Press, Berkeley.

ARCHIBALD, J. D., J. K. RIGBY, JR., AND S. F. ROBISON. 1983. Systematic revision of *Oxyacodon* (Condylarthra, Periptychidae) and a description of *O. ferronensis* n. sp. Journal of Paleontology 57: 53–72.

ARCHIBALD, J. D., R. M. SCHOCH, AND J. K. RIGBY, JR. 1983. A new subfamily, Conacodontinae, and a new species, *Conacodon kohlbergeri*, of the Periptychidae (Condylarthra, Mammalia). Postilla 191: 1–24.

BUTLER, R. F., AND E. H. LINDSAY. 1985. Mineralogy of magnetic minerals and revised magnetic polarity stratigraphy of continental sediments, San Juan Basin, New Mexico. Journal of Geology 94: 535–554.

CIFELLI, R. L. 1983. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). American Museum Novitates 2772: 1–49.

COPE, E. D. 1882a. Some new forms from the Puerco Eocene. American Naturalist 16: 833–834.

______. 1882b. Synopsis of the Vertebrata of the Puerco Eocene epoch. Proceedings of the American Philosophical Society 20: 461–471.

GAZIN, C. L. 1938. A Paleocene mammalian fauna from central Utah. Journal of the Washington Academy of Science 28: 271–277.

______. 1939. A further contribution to the Dragon Paleocene fauna of central Utah. Journal of the Washington Academy of Science 29: 273–286.

______. 1941. The mammalian faunas of the Paleocene of central Utah, with notes on the geology. Proceedings of the United States National Museum 91: 1–53.

GINGERICH, P. D., P. HOUDE, AND D. W. KRAUSE. 1983. A new earliest Tiffanian (late Paleocene) mammalian fauna from Bangtail Plateau, western Crazy Mountain Basin, Montana. Journal of Paleontology 57: 957–970.

KRAUSE, D. W., AND P. D. GINGERICH. 1983. Mammalian fauna from Douglass Quarry, earliest Tiffanian (late Paleocene) of the eastern Crazy Mountain Basin, Montana. Contributions from the Museum of Paleontology, University of Michigan 26: 157–196.

MATTHEW, W. D. 1937. Paleocene faunas of the San Juan Basin, New Mexico. Transactions of the American Philosophical Society, new series 30: 1–510.

OSBORN, H. F., AND C. EARLE. 1895. Fossil mammals of the Puerco beds. Collection of 1892. Bulletin of the American Museum of Natural History 7: 1–70.

RIGBY, J. K., JR. 1980. Swain Quarry of the Fort Union Formation, middle Paleocene (Torrejonian), Carbon County, Wyoming: geologic setting and mammalian fauna. Evolutionary Monograph 3. 178 pp.

ROBISON, S. F. 1986. Paleocene (Puercan-Torrejonian) mammalian faunas of the North Horn Formation, central Utah. Brigham Young University Geology Studies 33: 87–133.

ROSE, K. D. 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. University of Michigan Papers on Paleontology 26: 1–196.

SIMPSON, G. G. 1936. A new fauna from the Fort Union of Montana. American Museum Novitates 873: 1–27.

______. 1937a. The Fort Union of the Crazy Mountain Field, Montana, and its mammalian faunas. Bulletin of the United States National Museum 169: 1–287.

______. 1937b. Additions to the upper Paleocene fauna of the Crazy Mountain Field. American Museum Novitates 940: 1–15.

______. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85: 1–350.

SPIEKER, E. M. 1960. The Cretaceous-Tertiary boundary in Utah. 21st International Geological Congress, Copenhagen 5: 14–24.

TOMIDA, Y. 1981. "Dragonian" fossils from the San Juan Basin and status of the "Dragonian" land mammal "age." Pages 222–241 *in* S. G. Lucas, J. K. Rigby, Jr., and B. S. Kues, editors, Advances in San Juan Basin paleontology. University of New Mexico Press, Albuquerque.

______. 1982. A new genus of picrodontid primate from the Paleocene of Utah. Folia Primatologica 37: 37–43.

TOMIDA, Y., AND R. F. BUTLER. 1980. Dragonian mammals and Paleocene magnetic polarity stratigraphy of the North Horn Formation, central Utah. American Journal of Science 280: 787–811.

VAN VALEN, L. 1967. New Paleocene insectivores and insectivore classification. Bulletin of the American Museum of Natural History 135: 217–284.

______. 1978. The beginning of the Age of Mammals. Evolutionary Theory 4: 45–80.

WEST, R. M. 1971. Deciduous dentition of the early Tertiary Phenacodontidae (Condylarthra, Mammalia). American Museum Novitates 2461: 1–37.

______. 1976. The North American Phenacodontidae (Mammalia, Condylarthra). Contributions to Biological Geology, Milwaukee Public Museum 6: 1–78.

WOOD, H. E., II, R. W. CHANEY, J. CLARK, E. H. COLBERT, G. L. JEPSEN, J. B. REESIDE, JR., AND C. STOCK. 1941. Nomenclature and correlation of the North American continental Tertiary. Bulletin of the Geological Society of America 52: 1–48.

Received 6 May 1994
Accepted 12 December 1994